

BULBIFEROUS *ACONITUM* (RANUNCULACEAE) OF THE WESTERN UNITED STATES

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ABSTRACT

Aconitum columbianum Nutt. is a large and morphologically variable complex of populations extending from southern Canada to northern Mexico, and from California to New York. Bulbiferous populations have a restricted distribution, occurring in the Cascade Range from northern to southern Oregon, in the Klamath Mountains of northern California, and with a small, disjunct group in the California Sierra Nevada south of Lake Tahoe. These bulbiferous aconites are probably the most distinctive group within the *A. columbianum* complex, and they are treated herein as a subspecies.

RESUMEN

Aconitum columbianum Nutt. es un complejo grande y variable morfológicamente de poblaciones que se extienden desde el sur de Canadá hasta el norte de México, y desde California hasta Nueva York. Las poblaciones bulbíferas tienen una distribución restringida, encontrándose en la Cordillera de la Cascada desde el norte al sur de Oregón, en las Montañas Klamath del norte de California, y un pequeño grupo disyunto en al sur del Lago Tahoe en la Sierra Nevada de California. Estos acónitos bulbíferos son probablemente el grupo más distintivo dentro del complejo *A. columbinum*, y aquí son tratados como una subespecie.

KEY WORDS: *Aconitum columbianum*, bulbifery, taxonomy, distribution.

INTRODUCTION

Aconitum columbianum Nutt. is a polymorphic complex of populations occurring in the mountains of western North America from British Columbia, Canada to Chihuahua, Mexico and from California to South Dakota. Disjunct, outlying populations of *A. columbianum* occur also in the Driftless area of Iowa and Wisconsin (Brink 1982), and in Ohio and New York (Brink & Woods submitted for publication; Iltis 1965). Previous investigations indicated extreme differences among regional groups of populations, particularly in floral morphology and other correlated characters. This variation was continuous, however, with no clearly defined breaks, if populations throughout the range of the species were considered in aggregate (Brink

1975, 1980, 1981, 1982; Brink & deWet 1980). Bulbiferous populations were somewhat different in this regard since they appeared to be consistently distinct from all other *A. columbianum*. The purpose of this investigation was to determine the geographical distribution of these bulbiferous aconites, and to review the taxonomy of this group.

MATERIALS AND METHODS

Aconitum populations of the United States were compared in field, herbarium, laboratory, and uniform nursery investigations. Geographical distribution of bulbiferous populations was determined by field investigation and by mapping locations from herbarium specimens (CAS, CHSC, CLM, ILL, JEPS, OSC, RM, UC, US, UTC, WILLU, WS). *Aconitum* plants from bulbiferous and non-bulbiferous populations were transplanted and grown in growth chambers and greenhouses to study bulbil production under controlled conditions.

RESULTS

In field investigations we found no intergradation between bulbiferous and non-bulbiferous *Aconitum columbianum* (however, see Hitchcock et al. 1964; Abrams 1944). The populations that we have seen were either bulbiferous, with all plants of sufficient size and maturity producing conspicuous bulbils in the leaf axils, or they were completely non-bulbiferous with no bulbil producing plants. In growth chambers and greenhouses, only plants from bulbiferous populations produced bulbils. Bulbils were illustrated in Brink (1980) and Hickman (1993).

Bulbils are an effective means of vegetative reproduction. In natural populations they fall to the ground late in the season where they sprout vigorously, giving rise to new plants. A single leaf axil may produce one or more bulbils. Bulbil production usually is greatest at about the middle of the aerial stem, and diminishes toward the top and bottom of the plant. Most bulbiferous plants bear both bulbils and flowers. On a small percentage of plants, however, bulbifery completely supplants flower production, and bulbils are produced to near the apex of the terminal inflorescence, in place of flowers. A more in-depth description of bulbifery can be found in Brink (1975). Bulbil production should not be confused with the production of one to several small daughter tubers at the first few nodes above the parent tuber, usually below ground. This occurs on a small percentage of the plants in all bulbiferous and non-bulbiferous populations.

Bulbiferous *Aconitum columbianum* have a restricted distribution (Fig. 1), with one group of populations occurring in the Sierra Nevada mountains of California south of Lake Tahoe in El Dorado, Amador and Alpine counties;

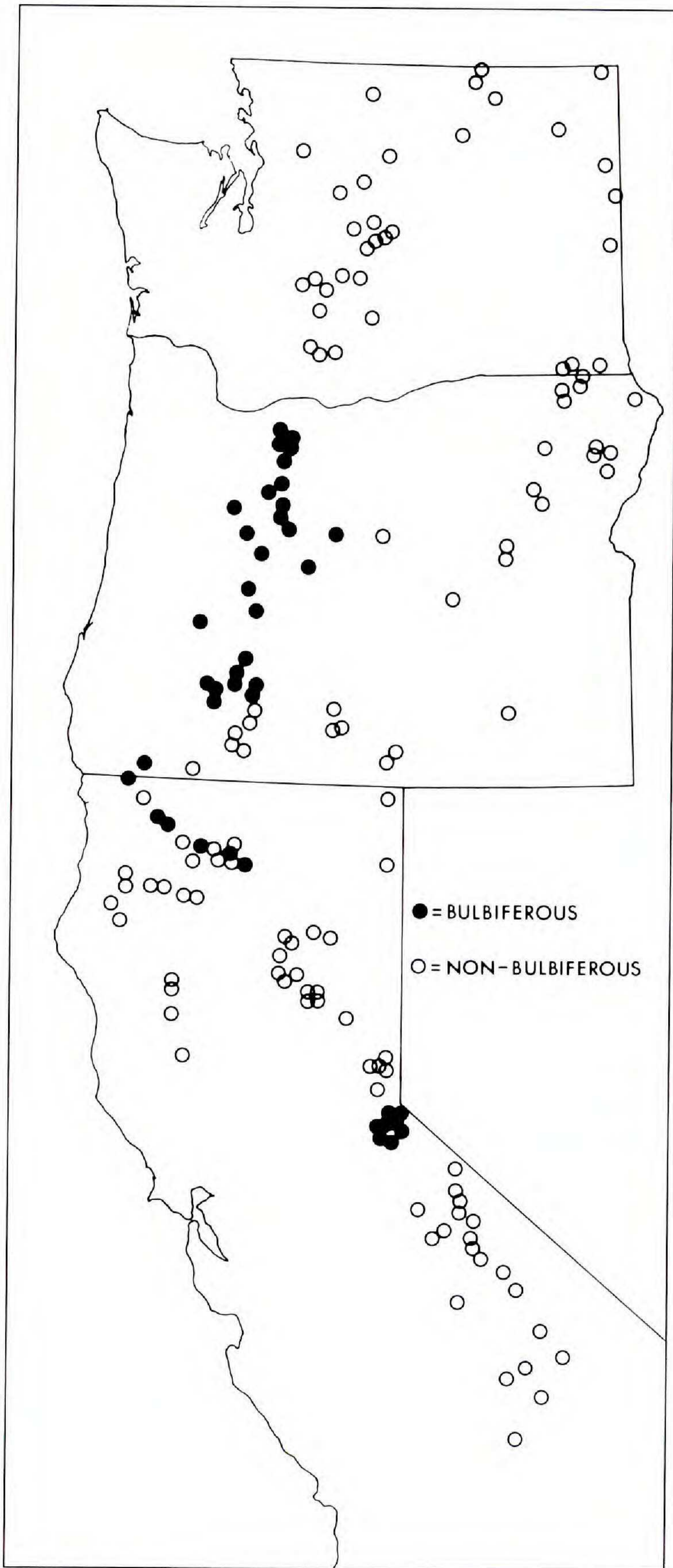


FIG. 1. Distribution of bulbiferous *Aconitum columbianum*.

and another group beginning ca. 350 miles away in northern California in the Klamath Mountains of Siskiyou and Del Norte counties. Bulbiferous populations extend from southern to northern Oregon in the Cascade range in Josephine, Jackson, Klamath, Douglas, Lane, Deschutes, Linn, Jefferson, Marion, Clackamas, Wasco, and Hood River counties.

Munz and Keck (1968) were uncertain whether the two disjunct groups of bulbiferous *Aconitum* in California (Fig. 1) should be treated as separate taxa. We can discern no consistent morphological features separating these two groups (Brink 1975).

DISCUSSION

We have decided to treat bulbiferous *Aconitum columbianum* at the subspecific level, due in part to the nature of the variation within the species as a whole. The *A. columbianum* complex is extremely polymorphic (Brink 1980, 1982; Brink & de Wet 1980). The existence of geographical races led to a proliferation of published names at the specific, subspecific and varietal levels. This nomenclatural proliferation was often the result of regional studies, which did not consider patterns of variation within the entire *Aconitum columbianum* complex. Geographical races that appear quite distinct within a regional context may be indistinguishable from other races occurring hundreds or even thousands of miles away. Robust and diminutive races that are regionally distinct are "connected" by intermediate races if the entire range of the species is considered (Brink 1980, 1981, 1982).

We have treated *Aconitum columbianum* as one, large, polymorphic, intergrading complex. Only one group of populations is consistently distinct from all others. These are the bulbiferous aconites, which occur in California and Oregon. We have chosen to distinguish this group as a subspecies because it is geographically and morphologically distinct. Recognition of these bulbiferous aconites at the species level would not seem to be warranted, especially since we have not accorded formal taxonomic recognition to regional variants that are exceedingly diverse, but in characters that intergrade throughout the range of the complex (Brink 1982).

TAXONOMIC TREATMENT

Aconitum columbianum Nutt. in Torrey and Gray, Fl. N. Amer. 1:34. 1838.

Tuber to ca. 6 × 1.5 cm; "parent" tuber produces 1 (rarely 2) "daughter" tubers with a connective so short the tubers are essentially contiguous. **Stem** erect and stout to twining and reclining, 2–30 dm long. **Leaves** 5–15 cm broad, deeply 3–5 (7) cleft, lobes variously incised and toothed. **Inflorescence** racemic, terminal, or terminal and axillary. **Flowers** typically deep

purple to blue, occasionally white, yellowish, or blue-tinged; 18–50 mm high, helmet 11–34 mm high, pendent sepals 6–16 mm long.

KEY TO SUBSPECIES

- 1a. Without bulbils in leaf axils or inflorescence subsp. *columbianum*
 1b. With conspicuous bulbils in leaf axils and/or inflorescence subsp. *viviparum*

1a. *Aconitum columbianum* subsp. *columbianum*

Aconitum arizonicum Greene; *A. bakeri* Greene; *A. cheirophyllum* Greene; *A. columbianum* var. *bakeri* Harrington; *A. columbianum* var. *lutescens* M. E. Jones; *A. columbianum* var. *ochroleucum* A. Nelson; *A. columbianum* subsp. *pallidum* Piper; *A. divaricatum* Rydberg; *A. geranioides* Greene; *A. glaberrimum* Rydberg; *A. gracilentum* Greene; *A. helleri* Greene; *A. infectum* Greene; *A. insigne* Greene; *A. leibergii* Greene; *A. lutescens* A. Nelson; *A. macilentum* Greene; *A. mogollonicum* Greene; *A. noveboracense* A. Gray; *A. noveboracense* var. *quasiciliatum* Fassett; *A. ochroleucum* Rydberg; *A. obtusiflorum* Greene; *A. patens* Rydberg; *A. porrectum* Rydberg; *A. ramosum* A. Nelson; *A. robertianum* Greene; *A. subcaesium* Greene; *A. tenue* Rydberg; *A. tricornis* Greene; *A. uncinatum* subsp. *noveboracense* (A. Gray) Hardin; *A. vestitum* Greene.

Spring-fed bogs, seep areas, meadows, along streams, and in other wet areas in the mountains of western North America from British Columbia, Canada to Chihuahua, Mexico at elevations of ca. 900–4,000 m. Brit. Col., Wash., Ore., Calif., Nev., Mont., Idaho, Utah, Ariz., S. Dak., Wyo., Colo., and N. Mex. Disjunct, outlying, populations occur at lower elevations (as low as 300 m), in Iowa, Wisconsin, Ohio and New York.

Chromosome Number: $n = 8$ [Wiens & Halleck 1962, Cates 1968], $2n = 16$ [Longacre 1942, Kawano 1965, Crawford & Gardner 1974, Brink 1975], $2n = 18$ [Crawford & Gardner 1974].

1b. *Aconitum columbianum* subsp. *viviparum* (Greene) Brink comb.

NOV. BASIONYM: *A. viviparum* Greene, Feddes Repert. Spec. Nov. Regni Veg. 7:2. 1909. TYPE: OREGON: swamps near Crater Lake, southern Oregon, *Cusick* 2972 (LECTOTYPE, designated herein: WS!; ISOLECTOTYPE: UC!).

Aconitum bulbiferum Howell, Fl. NW Amer. 1:25. 1897. Non *A. bulbiferum* Reichenbach, Übers. Acon. 55. 1819. *A. howellii* Nels. & Macbr., Bot. Gaz. 56:473. 1913. *A. columbianum* var. *howellii* (Nelson & Macbride) C.L. Hitchcock, Vasc. Pls. Pacif. NW 2:231. 1964. OREGON: marshes eastern slope Cascade Mountains near Mt. Hood, *Howell*.

A. hanseni Greene, Feddes Repert. Spec. Nov. Regni Veg. 7:3. 1909. CALIFORNIA. Amador Co.: Hope Valley, 1892, *George Hansen*. [Note: Hope Valley is actually in Alpine County.]

A. platysepalum Greene, Feddes Repert. Spec. Nov. Regni Veg. 7:2. 1909. CALIFORNIA: S side Mt. Shasta, northern California, Jul 1897, *H.E. Brown*.

Spring-fed bogs, seep areas, meadows, along streams, and in other wet areas at elevations of ca. 900–2,500 m in the Cascade Range from northern to southern Oregon, in the Klamath Mountains of northern California, and

with a small disjunct group of populations in the California Sierra Nevada south of Lake Tahoe.

These bulbiferous aconites were first distinguished as *Aconitum bulbiferum* Howell in 1897, but this name is rejected as a later homonym of *A. bulbiferum* Reichenbach, which is part of *A. variegatum* L., a European aconite. Three specific names were published simultaneously in 1909 by E.L. Greene for bulbiferous *Aconitum*. One of these names (*A. viviparum*), was chosen to serve as the basionym for the new subspecific combination, which refers to all bulbiferous *Aconitum columbianum*. The lectotype was chosen from among the syntypes of the basionym.

Bulbiferous populations in California have small flowers and shallow nectaries (Brink 1975), and we suspected that this would be the case for all bulbiferous *Aconitum columbianum*. We found, however, that bulbiferous aconites in the Mount Hood region of Oregon, at the northern extreme of the range of bulbiferous populations, have relatively large flowers and deep nectaries.

Flower color in *A. columbianum* is typically deep purple to blue; however, color variants include completely white, yellowish, cream-colored, or blue-tinged at the edges of the sepals. Color variants occur occasionally within blue-flowered populations, but there are also white-flowered populations, and groups of populations. For example, a group of white-flowered, non-bulbiferous populations occurs in northeast Oregon and southeast Washington. Consequently, it is not surprising that there are also white-flowered bulbiferous populations, which occur in Alpine and Amador counties of California (see Representative Specimens, below).

Chromosome number: $2n = 18, 19, 20$ [Brink 1975].

Representative Specimens: *Aconitum columbianum* subsp. *viviparum*: **CALIFORNIA.** **Alpine Co.:** Hope Valley, 29 Aug 1974, *Brink & Mayer s.n.* (CHSC) [flowers white, blue-tinged at edges]. **Amador Co.:** E of Silver Lake Dam, 14 Aug 1982, *McNeal 2750* (OSC) [white-flowered]. **Del Norte Co.:** Dunn Creek, 6 Aug 1938, *Keck 4793* (DS). **El Dorado Co.:** Lily Lake, 12-14 Aug 1978, *Brink 1469* (CHSC); Echo Summit, 29 Aug 1974, *Brink & Mayer s.n.* (CHSC). **Siskiyou Co.:** Red Rock Creek, 26 Jul 1974, *Brink & Brink s.n.* (CHSC); Kangaroo Lake and vicinity, 24 Jul 1974, *Brink s.n.* (CHSC). **OREGON.** **Clackamas Co.:** Clackamas Lake, 24 Jul 1927, *Peck 15852* (DS). **Deschutes Co.:** Tumalo Creek, 12 Aug 1906, *Whited 3162* (OSC). **Douglas Co.:** Diamond Lake, 17 Jul 1924, *Applegate 4134* (OSC). **Hood River Co.:** Barlow Pass, Mount Hood, 31 Jul 1934, *Thompson 11208* (US). **Jackson Co.:** Woodruff Meadows, 26 Jul 1925, *Pendleton s.n.* (OSC). **Jefferson Co.:** Camp Sherman, 27 Aug 1962, *Schoth 1929* (OSC). **Josephine Co.:** Lake Creek, Siskiyou Mountains, 18 Jul 1949, *Whittaker SS217* (WS). **Klamath Co.:** Pole Bridge, Crater Lake Park, 31 Jul 1922, *Applegate 3413* (UC). **Lane Co.:** Gold Lake, 1 Sep 1962, *Dennis 2433* (UTC). **Linn Co.:** Monument Peak, 9 Aug 1947, *Aller s.n.* (OSC). **Marion Co.:** Olallie Meadow, 9 Aug 1978, *Dawn 63* (OSC). **Wasco Co.:** Barlow Road, 1 Sep 1964, *French 2604* (OSC).

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